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3.2.4 Seasonal patterns and interannual variability of phytoplankton in Lake Stechlin (1994-2003)

Saisonale Muster und interannuelle Variabilität des Phytoplanktons im Stechlinsee

Key words: deep oligo-mesotrophic lake, phytoplankton, picoplankton, DCM, succession, species composition, global climate change, Water Framework Directives

Abstract

The paper presents results of detailed phytoplankton investigations in Lake Stechlin between 1994 and 2003. The analysis includes the picoplankton fraction (dominated by Cyanobium sp.) that regularly appears as a deep-layer chlorophyll maximum (DCM). Planktothrix and Aulacoseira are successful competitors against Cyanobium in the isothermal period, the consequences differ markedly due to the fact that Planktothrix is able and Aulacoseira is unable to accumulate in the DCM after the onset of thermocline. The „regular-Cyanobium" and „irregular-Planktothrix, -Aulacoseira" patterns of DCM development has a basic influence on ecosystem functioning. Lake Stechlin a pristine, oligo-mesotrophic deep lake, with an established and detailed monitoring system and thus has been an ideal reference site for studying the influence of global climate changes on plankton that may improve our predictive tools for impact assessment.

Zusammenfassung

Es werden Resultate detaillierter Phytoplanktonstudien am Stechlinsee in den Jahren 1994 bis 2003 dargestellt. In die Untersuchungen wurde auch die Picoplanktonfraktion (dominiert von Cyanobium sp.) mit eingeschlossen, die regelmäßig als Tiefenchlorophyllmaximum (DCM) erscheint. Erfolgreiche Konkurenten um die Wachstumsressourcen von Cyanobium sp. sind Planktothrix und Aulacoseira, wobei Planktothrix während der Sommerstagnation das DCM prägen kann, Aulacoseira aber nicht. Die dabei auftretenden „regulären- Cyanobium" und „irregulären-Planktothrix, -Aulacoseira" Entwicklungsmuster des DCM haben maßgeblichen Einfluss auf die Funktion des Ökosystems. Der Stechlin als klarer, oligo- bis mesotropher tiefer See ist in einem detailliertem Monitoringsystem integriert. Er ist ein ideales Referenzgewässer zum Studium des Einflusses globaler klimatischer Veränderungen auf Plankton und zur Erarbeitung von Methoden des „impact assesments".

3.2.4.1 Introduction

The phytoplankton of Lake Stechlin has been studied more or less regularly since 1959. Results for 1973 and 1975 were published by the original investigator (Küchler 1981, 1982), while data for periods 1959-1962, 1963-1964 and 1969-1972 appeared in the syntheses by Casper (1985 a, b). The latter contained a checklist of the algal flora of Lake Stechlin. Data for 1992 have been published by Krienitz & Scheffler (1994). Extensive measurements on chemical variables and primary production of phytoplankton were initiated in 1970 (Koschel 1981, 1985, 1995; Koschel et al. 2002; Mothes et al. 1985). Because of methodological differences between early (1950s –1970s) quantitative phytoplankton studies and recently applied methods, direct comparisons cannot be made (Padisák et al. 1998), however, historical descriptions suggest quite a high level of constancy in phytoplankton patterns even with its sometimes surprising deviations.

Since 1994, a regular sampling program has been carried out which includes physical and chemical properties of water, primary production, phytoplankton and zooplankton studies. After the recognition of a deep chlorophyll maximum (DCM) in the upper hypolimnion (Padisák et al. 1997; Gervais et al., 1997), this phytoplankton fraction was also included in weekly/biweekly samplings. Because of their relatively high share in annual biomass production, centric diatoms were also monitored at the species-specific level (Scheffler & Padisák 1997, 2000).

The present synthesis reports on the phytoplankton changes observed between 1994 and 2003. The interannual comparison presented in this paper allows us to reach conclusions about regular and irregular successional events and their possible reasons in the context of recent theories in community ecology.

3.2.4.2 Material and methods

Samples from 10 depths evenly distributed within the 0-25 m layer were taken at a sampling site located at the maximum depth of the lake. These samples were integrated for regular phytoplankton counts, and were analyzed as depth-specific subsamples to asses abundance of the most important species involved in DCM: *Cyanobium sp.* and *Planktothrix rubescens*. Phytoplankton was counted in an inverted microscope, and autotrophic picoplankton (APP) on black membrane filters using autofluorecsence. Chemical measurements followed internationally acknowledged methods. For more details on sampling and methods see Padisák et al. (2003a, 2003b).

3.2.4.3 Results and discussion

In comparison with other deep oligotrophic lakes in similar geographic regions (Padisák et al., 1998), the phytoplankton flora of Lake Stechlin is very rich.

Phytoplankton flora

In quantitative samples taken in the period 1994-2003, 189 planktonic species were identified, however, in individual years, 96-130 species were found (Figure1).

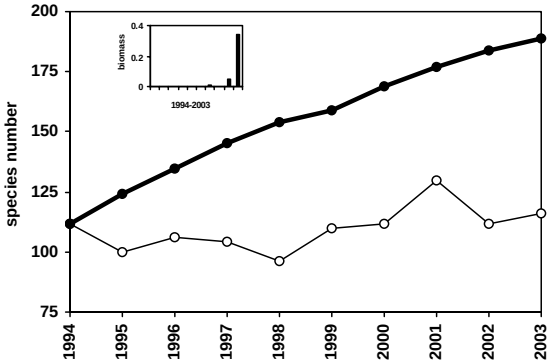

Fig. 1: Number of species found annually (○) in Lake Stechlin in years between 1994 and 2003, and the cumulative species number (●) for the same period. Subgraph (black bars): annual average biomass (µg L^{-1}) of *Aphanizomenon flos-aquae*.

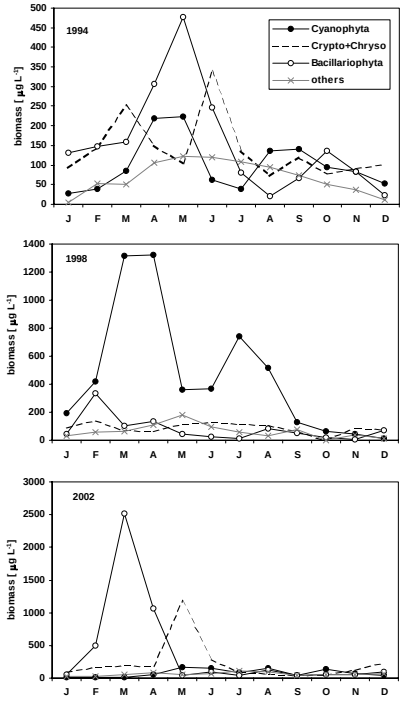

Fig. 2: Biomass (µg L^{-1}, data represent monthly averages) of the main phytoplankton groups in Lake Stechlin in 1994, 1998 and 2002. Successional sequences correspond to the pattern i), ii) and iii) described in the text.

According to the principles of Island Biogeography, cumulative species number (Figure 1) ought to provide a logarithmic-type of saturation (less and less "new species" are found per unit effort) supposing that "new species" occur only because their density is so low that they need a large sample size to be noted. Instead, cumulative species number shows a linear increase (R^2=0.989) that indicates that the relationship is instead, due to a continuous introduction/extinction. Most such species appear and disappear, however, some manage to establish permanent populations in the lake. The best example, probably, is *Aphanizomenon flos-aque* that occurred first in 2000, and has been exhibiting an apparently exponential growth (subgraph of Figure 1). Ordination (Jaccard index of similarity for binary data, UPGMA fusion algorithm; Podani, 2000; Figure 3 A) shows, however, that floristic changes are slow and occur quite gradually; the separation of years 2002-2003 will be discussed later.

Vertical habitat utilization

Lake Stechlin has been an oligo-mesotrophic lake that is typically stratified between the end of May and October-November. In the stratified periods (summer), the concentration of dissolved key nutrients (N and P) fall below the limit that is considered limiting for phytoplankton growth (Sas, 1989), moreover, euphotic depth is deeper than mixing depth. This physico-chemical property divides the euphotic region to two contrasting habitats: one is a severely nutrient limited but light-saturated layer down to the mixing depth, and the other is a less nutrient deficient but low light layer between the mixing and the euphotic depth (Padisák et al. 2003a, b). Consequently, the lake offers an ideal habitat for development of a classical phytoplankton assemblage typical for oligotrophic deep lakes within the mixed layer and a DCM below. The extent and functional role of these two compartments is different since these factors largely depend on annual species-specific interactions prior to the onset of stratification.

Characteristics of the seasonal succession

Since concentrations of the key nutrients exceed the limiting level after the autumnal overturn, the main phytoplankton growth goes on in the period November-March when the lake is isothermal and can be considered as a continuously turbulent, cold, severely light-limited habitat. Under such conditions only cold- and shade adapted species are favored such as diatoms and cyanobacteria. During the 10-y inter-annual studies the following scenarios occurred in this period (Figures 2, 3):

i. Small-sized planktonic diatoms (*Cyclotella tripartita* and/or *C. pseudocomensis*; Scheffler & Padisák, 1997, Scheffler et al., 2003) grew together with the picoplanktonic *Cyanobium* sp. (and the also picoplanktonic green algae) in January-April. Then, parallel with the onset of stratification, diatoms (and green picoplankton) sank to the hypolimnion (Padisák et al. 2003c) and *Cyanobium* occupied the DCM layer (1994-1997).

ii. Small planktonic diatoms grew together with the picoplanktonic *Cyanobium* sp. (and the also picoplanktonic green algae) and *Planktothrix rubescens*. The former in January-April, and *P. rubescens* since the preceeding summer. Then, parallel with the onset of stratification, diatoms sank and *Planktothrix rubescens*, and to some extent, *Cyanobium* occupied the DCM (1998).

iii. *Aulacoseira islandica* (a large, chain-forming diatom) grew in the period November-February, and since the population exhausted the nutrients the *Cyanobium* growth was insignificant. Since *Aulacoseira* is heavy, it sank earlier than small centric diatoms (March-early April) because the lake was still quasi-isothermal, *Cyanobium* started to grow, however the DCM was able to form much later than in other years (2000-2003). In 2001-2002 species typically occurrig in the clear-water phase (predominantly chrysophytes and other small flagellates) provided a spring peak after *Aulacoseira* established.

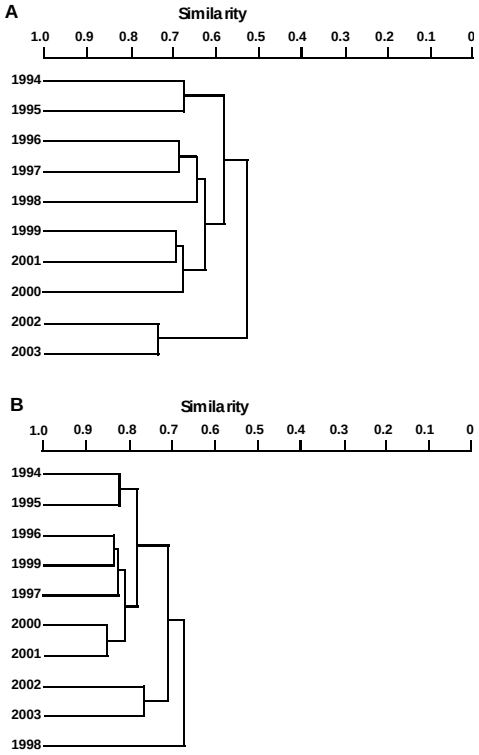

Fig. 3: Dendrograms of cluster analyses of phytoplankton data from Lake Stechlin in the period 1994-2003. A) Floristic similarity measured by Jaccard index based on binary data and B) Compositional similarity measured by Bray-Curtis index on basis of annual average biomass of species.

The feature of the lake divergent from the only-existing coherent plankton succession model, the PEG model (Sommer et al. 1986) is that decline of the spring phytoplankton maximum and the consequent clear-water phase was due to sinking of diatioms (whatever kind) to epilimnion, and not to zooplankton grazing (since the latter element of plankton starts to increase in June; Padisák et al. 2003b, c). The clear-water phase is short (June) in the case of scenario i) and ii), but long (April-June) in case of scenario iii). The growth of the typical summer assemblage culminated in July-August with dominance of large buoyant cyanobacterial species in the mixed layer (*Anabaena lemmermannii* + other nostocalean species; such as *Coelosphaerium kuetzingianum* and other large sized colonial chroococcaleans), very motile dinoflagellates (*Ceratium* and large *Peridinium*) and green algae with thick mucilage/motility (Willea, Quadrigula/Pseudosphaerocystis). When the thermocline starts to deepen, pennate diatoms (especially *Asterionella formosa* and *Fragilaria crotonensis*) appear in larger amounts accompanied by planktonic desmids. In October-November, *Rhodomonas minuta* and *R. lens* temporarily are dominant.

Ordination (Bray-Curtis index of similarity for biomass data, UPGMA fusion algorithm; Podani, 2000; Figure 3 B) of the data separates the year 1998 with predominance of *Planktothrix rubescens*, and the period 2002-2003 with *Aulacoseira* with spring chrysophyte maximum.

The average monthly phytoplankton biomass (Figure 4) was < 1 mg L^{-1} in years 1994-1997 and in 1999. In the 1998 when *Planktothrix* predominated, and in the first 2 years (2000, 2001) of *Aulacoseira* dominance, it increased to 1-2 mg L^{-1} and in the last 2 years (2002, 2003), also with *Aulacoseira* dominance, it exceeded 2 mg L^{-1}. Although Lake Stechlin has been traditionally considered as an oligotrophic lake, it is more appropriate to consider an oligo-mesotrophic lake, which is also supported by other measures (Koschel et al. 2002; Gonsiorczyk et al. 2003).

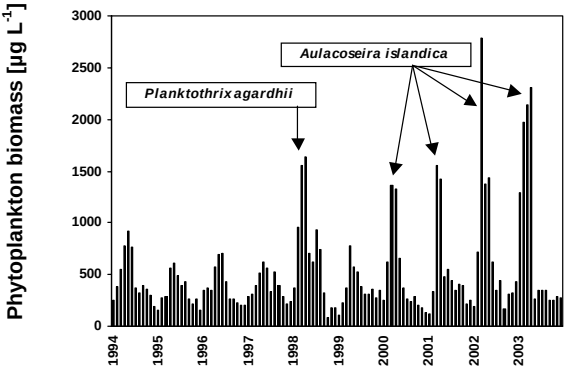

Fig.4: Phytoplankton biomass in the euphotic layer (0-25 m) of Lake Stechlin between 1994 and 2003. Data represent monthly averages.

The DCM of Lake Stechlin and its ecosystemic impact

One of the most characteristic features of phytoplankton in Lake Stechlin is the development of the DCM by *Cyanobium* sp. of picoalgal size. In the period 1994-1997 the *Cyanobium* sp. exhibited two peaks annually (Figure 5). The first occurred in April-May and was a consequence of layering of cells that developed during the isothermal period. The second was the result of in-situ growth in the DCM (Padisák et al. 1997).

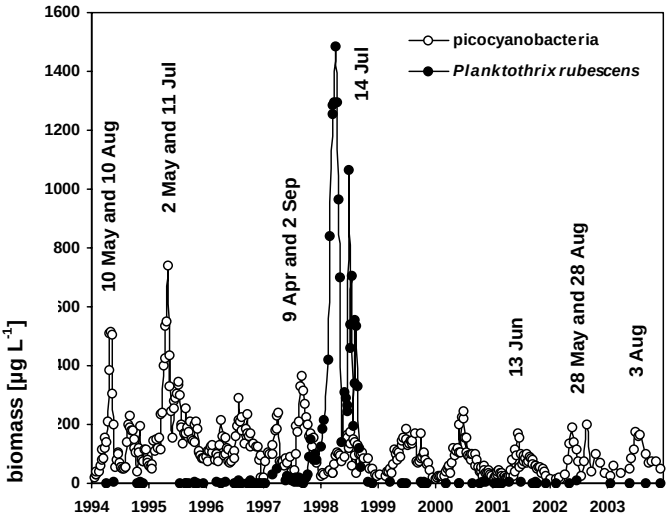

Fig. 5: Biomass (µg L^{-1}) of picocyanobacteria (dominant genus: *Cyanobium*) and *Planktothrix agardhii* in Lake Stechlin between 1994 and 2003. Data represent average of the upper 25 m which includes DCM. Dates in the graph-field indicate the timing of the annual maximum/maxima.

Planktothrix rubescens started to grow when the thermocline destabilized in the autumn of 1997, and did not stop growing during the isothermal period. Then part of the filaments sank to the hypolimnion and accumulated in the profundal region, another part formed a DCM. This winter *Cyanobium* failed to grow, and therefore the spring maximum could not be observed. Within the established DCM both *Planktothrix* and *Cyanobium* grew, and that resulted in a summer maximum of both. Based on ecophysiological adaptations of the two populations and in terms of Hardins's (1960) competitive exclusion principle, the populations reached a competitive equilibrium, with *Planktothrix* limited by P and *Cyanobium* by light (Figure 6).

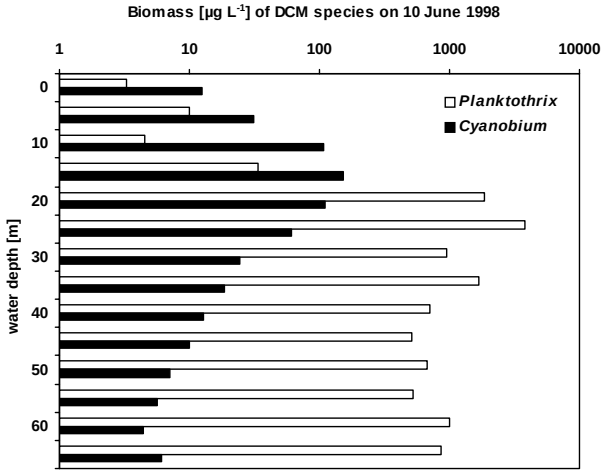

Fig. 6: Vertical distribution of *Cyanobium* and *Planktothrix* biomass (µg L^{-1}) on 10 June 1998 in Lake Stechlin. Note the logarithmic scale for biomass.

During the subsequent years (1999-2003) the only summer growth of *Cyanobium* was observed, in the latter 2 years apparently because early *Aulacoseira* growth exhausted P-pool of the lake. Although both *Planktothrix* and *Aulacoseira* are successful competitors against *Cyanobium* in the isothermal period, the consequences differ markedly due to the fact that *Planktothrix* is able, and *Aulacoseira* is unable, to accumulate in the DCM after the onset of thermocline.

In 1998 the *Planktothrix* growth had the following consequences: By the beginning of the stratification practically all the available key nutrients were trapped in large, ungrazeable filaments. Zooplankton growth (especially *Daphnia* and small cladocerans) in the summer was delayed and population density remained below the usual levels.

The usual spring diatom bloom was not observed. During growth of *Planktothrix*, dissolved inorganic nitrogen was almost always at limiting levels (Padisák et al. 2003b) which might have triggered a more intensive growth of *Anabaena lemmermannii*, the main N_2-fixing cyanoprokaryota species of the lake. *Anabaena* appeared in surface scums along the shores in 1998 which, being a toxin-producing species, might cause public health problems despite the overall low trophic status of the lake (Chorus & Bartram 1999).

A clear water stage did not appear at all in June 1998. The low biomass between the two *Planktothrix* peaks was a result of spatial positioning of *Planktothrix* cells. Chrysophytes that characterize the clear water phase were rare and their biomass was negligible.

As a consequence of the presence of a large *Planktothrix* population in the hypolimnion, there was an increased hypolimnetic oxygen deficit compared to other years (Padisák et al. 2003a) which might have had further consequences on the chemistry of the hypolimnion and transfer processes at the lake's sediment (Gonsiorczyk et al. 2001, 2003).

Summer Secchi transparency was significantly higher in 1998 than in other years. This, seemingly counterintuitive observation is easy to explain: since one "average" *Planktothrix* filament could compress approx. 55,000 *Cyanobium* cells, it is deducible that *Planktothrix* must have a much smaller light extinction coefficient per unit biomass than *Cyanobium*.

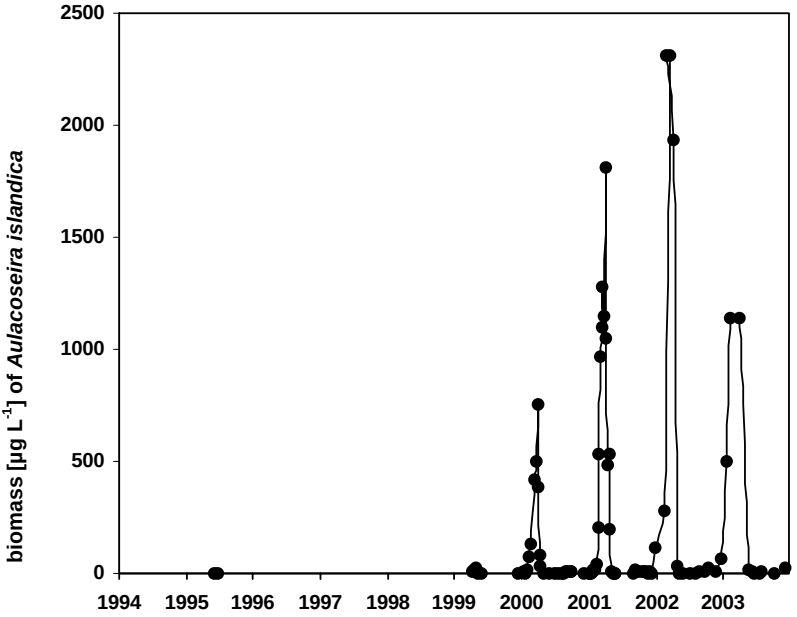

Fig. 7: Biomass (µg l^{-1}) of *Aulacoseira islandica* in Lake Stechlin between 1994 and 2003. Data represent average of the upper 25 m, inclusive of DCM.

If *Aulacoseira* is dominant in the spring, the above scenario does not take place. Spring growth of *Aulacoseira* is probably terminated by combined N+P+Si limitation during the isothermal period. At the very beginning of the thermocline heavy chains of *Aulacoseira* start to decrease fast but they are probably also start to disintegrate/decompose. The latter is indicated by the early peak of clear-water flagellates, most being mixotrophic. These flagellates "recover" a good deal of N and P previously assimilated by *Aulacoseira* for the summer phytoplankton. Moreover, their small and easily digestible cells provide an ideal nutritional basis for subsequent zooplankton growth.

In the context of the sudden appearance and/or disappearance of *Planktothrix* and *Aulacoseira* two basic questions may arise: where did they come from and why.

Planktothrix has been a permanent element of Lake Stechlin's flora although it usually maintains a low, perennial population (black dots on x axis of Figure 5 indicate occurrences). The year 1998 was not the first with recorded *Planktothrix* blooms. Historical data (Casper 1985b) report dense

populations in 1969-1972 and 1976-1978. The only "deviant" environmental variable prior to early and present blooms, has been the long-lasting, thick ice-cover in the preceding year.

The case of *Aulacoseira* is different. Prior to the period 1999-2001, the genus was found only in 2 consecutive samples in 1995. In 1999, the first viable chains occurred in the deepest profundal region of the lake (Padisák et al. 2003b, 2003c) and it gradually proliferated towards the epilimnion. This pattern indicates that the population originated from cysts buried in the sediments of the lake. Historical data do not report on such intensive growth of this species. Reasons for its success are unknown, however, it cannot be excluded that one irregular pattern (*Planktothrix* dominance beforehand) may shift the successional patterns that is considered "normal". However, we have to keep in mind that even a 10-y long intensive study is too short to prove or disprove such a deduction.

3.2.4.4 Conclusions

The long term phytoplankton studies in Lake Stechlin are unique in several respects, namely: historical data exist; the taxonomic resolution has been the most accurate that can be achieved by light microscopy; in adequate cases taxonomic resolution is further improved by other methods; picoplankton is included; furthermore primary production, as well as zooplankton density, physical and chemical measurements are included in the parallel monitoring programme. The regularity and accuracy of the above research activity facilitates a deep view into phytoplankton dynamics and so far resulted in many original findings on level of basic science.

More detailed papers on phytoplankton ecology in Lake Stechlin, as well as this short summary, make it clear that there are many questions connected to obvious results. Part of them are certainly connected to global climate-change cycles and trends, however, the 10-y period of intensive efforts has been too short a period to demonstrate these relationships.

In the recent past, many projects aimed to select relatively pristine "reference sites" exemplifying streams, lakes, coastal aquatic and terrestrial ecosystems (Water Framework Directive 2000). From 1966 to 1989 a nuclear power plant was operated in the Lake Stechlin area that resulted in thermal pollution, increased nutrient load (higher TP water from Lake Nehmitz), and intermittent destabilization of the stratification of the lake. Despite an increase in primary productivity, as demonstrated by Koschel et al. (2002) and despite the fact that the lake has recently been in a "recovery stage" from being a cooling water reservoir for a nuclear power station for almost 25 years, the lake has preserved its basically oligotrophic features and can be considered as a reference site for pristine, oligotrophic, deep lakes in the North German Lake District.

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